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Earthworm assemblages in urban habitats across biogeographical regions

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ABSTRACT

In urban landscapes, humans are the most significant factor determining belowground diversity, including earthworms. Within the framework of the Global Urban Soil Ecology and Education Network (GLUSEEN), a multi-city comparison was carried out to assess the effects of soil disturbance on earthworms. In each of five cities (Baltimore, USA; Budapest, Hungary; Helsinki and Lahti, Finland; Potchefstroom, South Africa), covering four climatic and biogeographical regions, four habitat types (ruderal, turf/lawn, remnant and reference) were sampled. The survey resulted in 19 species belonging to 9 genera and 4 families. The highest total species richness was recorded in Baltimore (16), while Budapest and the Finnish cities had relatively low (5–6) species numbers. Remnant forests and lawns supported the highest earthworm biomass. Soil properties (i.e. pH and organic matter content) explained neither earthworm community composition nor abundance. Evaluating all cities together, earthworm communities were significantly structured by habitat type. Communities in the two adjacent cities, Helsinki and Lahti were very similar, but Budapest clearly separated from the Finnish cities. Earthworm community structure in Baltimore overlapped with that of the other cities. Despite differences in climate, soils and biogeography among the cities, earthworm communities were highly similar within the urban habitat types. This indicates that human-mediated dispersal is an important factor shaping the urban fauna, both at local and regional scales.

1. Introduction

Globally, ~3500 earthworm species are known (Csuzdi, 2012). Although most of them have restricted ranges (Reynolds, 1994), a small (ca. 3%) percentage of the species are widely distributed. These earthworms are frequently associated with human activity (Lee, 1985) and are often called peregrine (Michaelsen, 1903) or anthropochorous (Gates, 1970) earthworms. Peregrine species are found in almost all families, but they are most common in the Holarctic Lumbricidae and the Oriental Megascolecidae with approximately 35 and 50 species, respectively (Blakemore, 2009).

Urbanization drastically alters soil physical and chemical properties as well as the associated soil biota (Wall et al., 2015). In cities, a range of soil conditions exists from relatively undisturbed soils, usually in remnant vegetation patches and old parks, to entirely engineered soils. These diverse conditions form a patchwork of soil habitats with some more or less favorable for the belowground biota.

At any given location, persistent community composition is determined by a multitude of abiotic and biotic factors, including the regional species pool, dispersal abilities of the taxa, environmental filters and biotic interactions. A large number of theories exist explaining diversity and composition of local community structure. Recently, Vellend (2010) proposed that a single general framework, involving four mechanisms, speciation, dispersal, drift, and selection, can

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Table 1
General geographical, climatic and soil characteristics of the five cities in this study.

Country/region	City	Location	Climate[a]	Parent material	Soil order[b]	Population
USA North America	Baltimore	39° 17′ 25.37″ N76° 36′ 43.88″ W	Humid-subtropical	Mafic rock	Ultisol	621,000
Hungary Central Europe	Budapest	47° 29′ 52.84″ N19° 02′ 23.68″ E	Warm summer continental	Dolomite	Alfisol	1,728,000
Finland	Helsinki	60° 10′ 10.27″ N24° 56′ 7.62″ E	Boreal	Granite	Spodosol	1,400,000
Northern Europe	Lahti	60° 58′ 57.61″ N25° 39′ 41.44″ E	Boreal	Granite/till	Spodosol	102,000
South Africa Southern Africa	Potchefstroom	26° 43′ 0.01″ S27° 06′ 0.00″ E	Dry winter subtropical highland	Shale/diabase	Aridisol	250,000

[a] Based on the Köppen climate classification system (Beck et al., 2018).
[b] Based on the USDA soil classification system.

accommodate all existing theories of community assembly. In the urban landscape, each of these processes has an anthropogenic element (Aronson et al., 2016; Swan et al., 2011). Historical land use, accidental or deliberate introduction and transport, as well as local management can either promote or prevent establishment of a species or higher taxonomic group. Aronson et al. (2016) proposed a framework in which these factors are arranged in a series of hierarchical filters, which then explain urban biodiversity at multiple scales.

Earthworms are a common component of urban soil fauna and in general, they are viewed as beneficial organisms improving soil conditions for plant growth. Recently, the high abundance of invasive earthworms, especially those in the family Megascolecidae, has been changing our perception of earthworms as 'beneficial' organisms (Hendrix et al., 2008). Invasive earthworm activity can lead to the loss of leaf litter and organic soil horizons (e.g. Ma et al., 2013; Szlavecz et al., 2018a), nutrients (Groffman et al., 2015) as well as shifts in microbial community composition (Chang et al., 2017). Additionally, earthworms have been shown to negatively affect native plants (Craven et al., 2017; Hale et al., 2006) and wildlife (Loss et al., 2012; Ransom, 2011). Regardless of their effect, earthworms are a crucial component of virtually all ecosystems.

Urbanization has been considered a major cause of local species extinction and a process leading to biotic homogenization (McKinney, 2006). The assumed similarity of urban biotic assemblages has also been attributed to human behavior that modifies their surroundings. The idea that humans cause environmental conditions to converge compared to "natural" and initial conditions has been articulated in the 'Urban Ecosystem Convergence Hypothesis' (Pouyat et al., 2003) and tested in several studies (Epp Schmidt et al., 2017; Groffman et al., 2017; Pouyat et al., 2015). Homogenization of urban communities has been studied in plants (Schwartz et al., 2006), microbes (Epp Schmidt et al., 2017, 2019), insect orders (Knop, 2016; Lizée et al., 2011) and birds (van Rensburg et al., 2009). Urban earthworms have been surveyed in several locations (e.g. Baker et al., 1997; Ferreira et al., 2018; Xie et al., 2018) but most studies were carried out in one city and on one or a few specific habitats, such as parks (Schlaghamerský and Pižl, 2009), remnant forests (Szlavecz et al., 2006), median strips (Tiho and Josens, 2007), urban gardens (Tresch et al., 2018), and residential yards (Smetak et al., 2007). To date, multi-city comparisons of soil invertebrates have only been conducted for a few arthropod taxa, such as springtails (Collembola, Joimel et al., 2019), woodlice (Isopoda, Szlavecz et al., 2018b; Vilisics et al., 2012), millipedes (Diplopoda, Vilisics et al., 2012) and ground beetles (Carabidae, Niemelä and Kotze, 2009). While efforts for continental scale mapping of earthworm diversity and abundance are underway (Rutgers et al., 2016), urban areas are usually left out from such large scale analyses, partially due to the heterogeneity of habitats within the urban landscape.

The Global Urban Soil Ecology and Education Network (GLUSEEN) was established to connect urban soil scientists, ecologists, and citizen scientists across geographical areas, climatic zones and biomes. Based on the level of disturbance and intensity of management, GLUSEEN has developed a matrix of soil habitat types (Pouyat et al., 2017). Using a unified methodology for habitat selection and sampling, multi-city comparisons have been made on soil properties (Pouyat et al., 2015) and microbial communities (Epp Schmidt et al., 2017). Here we report data on earthworm assemblages in five cities representing four climatic and biogeographical regions. In each city, four habitat types, replicated five times, were surveyed, resulting in a total of 100 sampling locations. The objectives of the study were to assess and compare earthworm communities at multiple spatial scales. Specifically, we pose the following questions: 1) How does soil habitat type affect earthworm community structure and abundance; 2) How do soil properties affect earthworm abundance and diversity, and 3) How similar are urban earthworm assemblages across regions? Based on existing knowledge we expected to see higher earthworm abundance in less disturbed habitat types as well as a high degree of community similarity among cities.

2. Material and methods

2.1. Study sites and design

In the GLUSEEN project, five cities, Baltimore (USA), Budapest (Hungary), Helsinki and Lahti (Finland) and Potchefstroom (South Africa), were selected. The geographical locations of these cities represent a broad range of climate, geology and human population density (Table 1), but within each city, all sampling locations were on the same parent material (Pouyat et al., 2015).

Based on two disturbance and three management levels, a matrix of habitat categories with underlying soil characteristics was established (Pouyat et al., 2017). In the present study, the following three of six possible urban soil habitat types were sampled:

(1) LOW disturbance–LOW management (REM: remnant soil): deciduous or coniferous forest, grassland;
(2) HIGH disturbance–MEDIUM management, (TURF: turf/lawn soil): public greenspace, turfgrass;
(3) HIGH disturbance–LOW management (RUD: ruderal soil): massive or fill soil.

In addition, a semi-natural habitat type (REF: reference soil) outside the cities was assigned as a reference for comparison. The REF sites were unmanaged (except for the 80 yr. cutting rotation of trees in Finland) with their undisturbed soils located outside the urban matrix that represented native soil type and biome typical of the region.

The soil habitat types approximately correspond to a continuum of anthropogenic effects from lowest to highest in the following order: REF < REM < TURF < RUD. Altogether 100 sites (5 cities × 4 soil habitat types × 5 replicate plots per habitat type) were sampled (for more details, see Pouyat et al., 2015, 2017).

2.2. Earthworm sampling and identification

In temperate regions, spring or fall are the best seasons to sample earthworms, especially for those living relatively close to the soil surface. This time of the year soil temperature is moderate and soil moisture high; these conditions favor earthworm activity. Several methods, including hand sorting, extraction using chemicals, and electroshocking exist for earthworm sampling. Each has advantages and limitations (Čoja et al., 2008). Conducting research in urban habitats presents additional constraints due to land ownership, access, and safety to environmental and human health (Szlavecz et al., 2011). We chose the hot-mustard extraction method (Butt and Grigoropoulou, 2010; Iannone et al., 2012), because it is non-destructive, environmentally safe, and can be adopted by citizen scientists, which is one of the goals of GLUSEEN (Pouyat et al., 2017). In medium dosages it is as efficient as hand sorting or the formalin method for detecting the most common species and biomass assessment (Čoja et al., 2008). Earthworms were sampled in each city in spring 2014 using five, 25 cm × 25 cm quadrats, arranged around each of the 100 GLUSEEN experimental plots (Pouyat et al., 2017). All vegetation and leaf litter were removed from the quadrats, then 3.5 L repellent liquid containing 15 g Colman's mustard powder were applied in two portions with 15 min interval. This dosage equals to 240 g mustard per m^2. Emerging earthworms were placed in 70% ethanol, preserved in 4% formaldehyde solution and later stored in 70% ethanol. Biomass ($g\,m^{-2}$) was determined on the preserved material. For species identification and nomenclature, keys by Csuzdi and Zicsi (2003) and Scherlock (2012) were used. Most juvenile specimens were identified to genus level, except the smallest juveniles that are reported at family level.

2.3. Soil properties

Soil properties, such as soil organic matter, pH, saturation percentage (SP) and $CaCO_3$ content were used to investigate possible differences in earthworm abundance and community structure at the city level. Protocols for sampling, processing and analyses as well as most results have been reported in Pouyat et al. (2015). The only previously unreported data here are SP and $CaCO_3$ content. SP refers to the mechanical constituents of soils, and is related to texture (Westerman, 1990). $CaCO_3$ content was measured with a calcimeter; the soil was mixed with diluted HCl solution and the volume of CO_2 released was determined (ISO 10693, 1995). We report all soil data as supplementary material (Table S1).

2.4. Data analyses

All statistical analyses were performed in R 3.6.1 (R Development Core Team, 2019) using the “ggplot2” (Wickham, 2016) and “vegan” (Oksanen et al., 2019) packages. Assumptions of normality and homoscedasticity of the residuals were verified visually using diagnostic plots.

To test for difference in soil properties among habitat types within cities, one-way ANOVAs were applied. Then, Least Significant Difference (LSD) tests were carried out for multiple comparisons.

Species richness and Hill's number (Hill, 1973) were calculated to estimate alpha diversity. Hill's number, also known as the effective number of species, enables the comparison of community diversity on a linear scale, avoiding misinterpretations spawned by nonlinearity of most diversity indices. Immature earthworms, treated as a separate category, were included in the community analyses because they often dominate samples.

General linear (LMs) and linear mixed models (LMMs) were used to assess the effects of habitat types and soil properties (SOM, pH, SP, $CaCO_3$) on earthworm diversity (species richness, Hill's number) and biomass for each city both separately and combined. In LMMs, the city variable was considered as a random effect to account for spatial dependence. We performed stepwise multiple-regression analysis with forward selection of the explanatory variables. After fitting the full models for each dependent variable, we used Akaike Information Criterion (AIC) to select the most parsimonious model. For beta diversity, multivariate homogeneity of group dispersions among soil habitat types was analyzed using the “betadisper” function. To determine whether species composition of earthworm assemblages differed among soil habitat types within cities and among biogeographical regions (city), permutational multivariate analysis of variances (PERMANOVAs, Bray-Curtis dissimilarity with 9999 permutations) were run. The Bray-Curtis dissimilarity matrix was used to create ordinations using non-metric multidimensional scaling (NMDS) for each data set in order to visualize these effects on earthworm community structure.

To gain insight into large scale patterns, including biotic homogenization, city scale species compositions were compared to the regional species pools. Regional species pools were determined using comprehensive checklists for each region surrounding a given city. Specifically, Reynolds (1974, 2015) was used for the Greater Baltimore Metropolitan Region while Terhivuo (1988) and Blakemore (2007) were used for Helsinki and Lahti as data sources. The earthworm fauna of Hungary consists of several zoogeographically distinct regions (Csuzdi and Zicsi, 2003); the most relevant for Budapest is the Pilis Mountains-Buda Hills area. For the multi-city comparison, hierarchical cluster analysis using the Baroni-Urbani and Buser similarity index with UPGMA clustering method was performed, implemented in the software package SYNTAX (Podani, 2001). This index is more sensitive to biogeographical differences because it takes into account not only shared presences but to a lesser degree, also shared absences (Baroni Urbani et al., 1978; Biondi et al., 2013; Ventura et al., 2014).

Potchefstroom was excluded from all statistical analyses because of the very low number of individuals.

3. Results

3.1. Earthworm diversity, biomass and species composition

The earthworm survey resulted in 19 species belonging to 9 genera and 4 families (Table 2). Species richness ranged from 0 to 7 species per plot. In Potchefstroom, only 12 juveniles of three taxa (one family, one genus and one species) were found, and all of them at TURF sites. The highest total number (16) of species was recorded in Baltimore with the highest total species richness (11) in TURF. Budapest and the two Finnish cities had relatively low (5–6) species numbers. Habitat type had a significant influence in Budapest and Lahti (Table 3), where TURF and REM sites had significantly higher species richness, respectively.

Hill's number, the effective number of species, ranged from 0 to 5.18 in cities. In general, Baltimore and Lahti showed higher values compared to the other two cities. With the exception of TURF sites, the effective numbers of species were < 2 in Budapest and Helsinki (Fig. 1A). Significant differences among soil habitat types were found in Helsinki and Lahti; RUD sites were less diverse compared to the other land use categories (Fig. 1A, Table 3).

Earthworm biomass ranged from 0 to 178.18 $g\,m^{-2}$ per plot. At the city scale, i.e. combining all habitat types, mean biomass per plot ($g\,m^{-2}$ ± SE) was very low (4.64 ± 1.06) in Budapest, compared to the other cities. Lahti had the highest mean biomass with 44.69 ± 12.65 per plot, followed by Helsinki (28.67 ± 7.75) and Baltimore (23.32 ± 9.23). In all cities, *Lumbricus terrestris* was the most abundant species, showing the highest relative biomass compared to other species. At the city scale, there was high variation within habitat types and a habitat effect was detected only in Lahti (Fig. 1B, Table 3), but the linear mixed model showed that REM and TURF sites had significantly higher biomass than REF sites ($t = 2.16$, $p = 0.034$ and $t = 2.38$, $p = 0.020$, respectively).

Community structure did not differ among habitat categories in Baltimore and Budapest (Fig. 2A-B), but did so in Helsinki and Lahti

Table 2
Species list of the earthworms for the four soil habitat types in the five cities. × indicates presence. REF: reference; REM: remnant; TURF: turf/lawn; RUD: ruderal. Abbr.: Abbreviation of species names used in Figs. 2 and 3.

Species	Abbr.	Functional group[a]	Baltimore				Budapest				Helsinki				Lahti				Potchefstroom[b]			
			REF	REM	TURF	RUD	REF	REM	TURF	RUD	REF	REM	TURF	RUD	REF	REM	TURF	RUD	REF	REM	TURF	RUD
ACANTHODRILIDAE																						
Dichogaster modiglianii (Rosa, 1893)	Dimo	Epigeic																			×	
Diplocardia caroliniana Eisen, 1899	Dica	Endogeic	×	×	×																	
LUMBRICIDAE																						
Allolobophora chlorotica (Savigny, 1826)	Alch	Endogeic			×																	
Aporrectodea caliginosa (Savigny, 1826)	Apca	Endogeic	×	×	×	×					×	×	×	×	×	×	×	×				
Aporrectodea rosea (Savigy, 1826)	Apro	Endogeic			×	×	×	×	×	×												
Aporrectodea limicola (Michaelsen, 1890)	Apli	Endogeic		×																		
Aporrectodea tuberculata (Eisen, 1874)	Aptu	Endogeic		×																		
Aporrectodea sp	Apsp	Endogeic	×	×	×	×	×	×	×	×											×	
Dendrobaena octaedra (Savigy, 1826)	Deoc	Epigeic									×	×			×	×		×				
Lumbricus castaneus (Savigy, 1826)	Luca	Epigeic		×	×	×		×					×									
Lumbricus rubellus Hoffmeister, 1843	Luru	Epi-endogeic		×	×	×								×		×	×	×				
Lumbricus friendi Cognetti, 1904	Lufi	Anecic		×																		
Lumbricus terrestris Linné, 1758	Lute	Anecic	×	×	×			×			×	×	×	×		×	×	×				
Lumbricus sp	Lusp	Epi-endogeic	×	×	×	×		×	×	×	×	×	×	×	×	×	×	×				
Lumbricidae sp	Lumbsp	Epi-endogeic	×		×	×					×	×										
Octolasion lacteum (Örley, 1881)	Ocla	Endogeic			×	×	×	×	×													
Octolasion sp	Ocsp	Endogeic				×																
MEGASCOLECIDAE																						
Amynthas sp	Amsp	Epi-endogeic		×																		
MICROCHAETIDAE																						
Microchaetidae sp	Misp	Endogeic																			×	
Total species richness			6	10	11	9	3	6	4	3	5	5	4	4	3	5	4	5	0	0	3	0

[a] Classification is based on Csuzdi (2012).
[b] Potchefstroom data were excluded from further analyses.

Table 3
Final general linear models explaining the diversity (species richness and Hill's number), biomass, and species composition of earthworm communities based on habitat type and soil variables in four cities. SOM: soil organic matter.

City	Response variable	Explanatory variable	F	p
Baltimore USA	Species richness			
	Hill's number			
	Biomass			
	Composition			
Budapest Hungary	Species richness	Habitat	4.84	0.016
		SOM	20.70	< 0.001
		$CaCO_3$	22.26	< 0.001
	Hill's number	SOM	25.73	< 0.001
		$CaCO_3$	4.57	0.047
	Biomass	SOM	5.32	0.034
		$CaCO_3$	5.70	0.029
	Composition			
Helsinki Finland	Species richness			
	Hill's number	Habitat	4.21	0.023
	Biomass			
	Composition	Habitat	2.05	0.035
Lahti Finland	Species richness	Habitat	2.67	0.083
	Hill's number	Habitat	3.70	0.038
	Biomass	Habitat	3.12	0.042
	Composition	Habitat	1.51	0.075

(Table 3, Fig. 2C-D). Species level differences were also detected: *Aporrectodea caliginosa* and *Lumbricus castaneus* had higher abundances in TURF, while *Dendrobaena octaedra* was collected exclusively at REM and REF, i.e. woodland sites. In Baltimore and Budapest, none of the measured variables affected earthworm community composition (Table 3).

3.2. Earthworm communities and edaphic properties

Soil characteristics varied considerably, often even within the same habitat type (Table S1). Carbonate ($CaCO_3$) content was high in Budapest, although no consistent patterns were found among soil habitat types. Saturation percentage, a proxy for clay content, was higher in REF and REM habitats in all cities except Potchefstroom.

Of the measured edaphic variables, diversity (species richness and Hill's number) and biomass of earthworms decreased with increasing SOM and $CaCO_3$ content of soils in Budapest (Table 3).

3.3. Multi-city comparison

Evaluating all cities together, earthworm communities were significantly structured by habitat type, but not by geographical location (PERMANOVA, Bray–Curtis dissimilarity by habitat type nested within city: $F = 1.98$, $R^2 = 0.07$, $p = 0.003$; habitat: $F = 3.97$, $R^2 = 0.15$, $p = 0.200$; Fig. 3). Communities in Helsinki and Lahti were very similar while Budapest clearly separated from the Finnish cities. Earthworm community structure in Baltimore almost completely overlapped with that of the other cities. Beta diversity, measured as multivariate dispersion in composition around group centroids, differed only marginally among soil habitat types ($F = 2.43$, $p = 0.073$), with RUD and REF having the highest within-group variances.

Cluster analysis separated the regional species pools of the three different regions: Northern Europe with boreal climate and coniferous forest biome, Central Europe with warm summer continental and broadleaf deciduous forests, and the Mid-Atlantic in North America with humid subtropical climate and broadleaf deciduous forests. Fauna of the cities clustered together irrespective of geographical location (Fig. 4). Within the urban group, Baltimore and Budapest, despite being on different continents, formed another cluster, joining the other two European cities, Helsinki and Lahti.

4. Discussion

The number of urban earthworm species was low in all cities. As expected, local communities were dominated by peregrine species that have been reported to exist in other urban environments (Table 4). The large similarity in urban earthworm faunas is partially due to the relative proximity of these cities, i.e. most studies were conducted in Europe. Species lists in Curitiba, Brazil (Ferreira et al., 2018) and Beijing, China (Xie et al., 2018) are quite different, indicating the need to extend the geographical scale of urban faunal studies.

Biomass variation was relatively high, similar to some previous studies (Raczuk and Pokora, 2008; Tiho and Josens, 2000; Xie et al., 2018). Tiho and Josens (2000) attributed this phenomenon in part to dependence of earthworm activity on soil moisture and temperature, which are known to vary highly locally (Savva et al., 2013). With the exception of Budapest, the city-scale averages of biomass were broadly similar to data in the literature (Pižl and Schlaghamerský, 2007; Smetak et al., 2007; Tiho and Josens, 2000). However, Xie et al. (2018) reported biomass of earthworms ($15.6 \pm 14.0\ g\ m^{-2}$) in residential areas of Beijing to be as low as that detected in Budapest. In accordance with our results, usually the highest mean biomass values have been found in urban parks and lawns that overlap to some extent with REM and TURF in the present study: “intensely used public lawns” in Basel, Switzerland ($280\ g\ m^{-2}$; Glasstetter, 2012); “unaffected lawns” in Brno, Czech Republic ($110.6\ g\ m^{-2}$; Pižl and Schlaghamerský, 2007); “urban lawns close to street” in Siedlce, Poland ($162.52\ g\ m^{-2}$; Raczuk and Pokora, 2008), and “urban parks” in Moscow, USA ($94.12\ g\ m^{-2}$; Smetak et al., 2007).

Land use change and management have been known to profoundly affect earthworm diversity both in agricultural (e.g. Feijoo et al., 2011; Paoletti, 1999) and urban (Talavera et al., 2020; Xie et al., 2018) settings. In the Finnish cities, in addition to alpha diversity metrics, species composition was also influenced by habitat type. RUD sites were the least diverse, presumably reflecting recent physical disturbance.

Although only marginally significant, within-group variance appeared to be highest at REF and RUD sites. Potential reasons of higher dissimilarity for earthworms in these soil habitat types are different. Reference (REF) sites are by definition very different due to climatic and edaphic conditions. The RUD category might reflect different conditions in different locations. For example, RUD includes recently disturbed soil that lost its structure and horizons due to recent or planned construction, or vacant lots, where building rubble of demolished buildings and a thin organic layer, transported elsewhere, form the soil profile. Depending on the time of last disturbance and subsequent human intervention, stochastic processes can dominate earthworm community assembly (Tiho and Josens, 2007), which may have led to greater differences between sites.

Earthworm abundance and species composition were highly variable at the local scale even within the same habitat type. In Brussels (Belgium), Tiho and Josens (2007) conducted a null model analysis to explain earthworm assemblages in fragmented grassy areas and found little evidence for biotic interactions to control community assembly. Stochastic processes, such as annual or seasonal climate variability may be more important, especially in disturbed, compacted and shallow soils such as grassy medians. Additional factors resulting in high local variability include: 1) the surrounding landscape, source of colonization, 2) the timing and nature of disturbance on RUD sites, and 3) site maintenance, such as frequency of mowing, which affects soil moisture, temperature and N input.

The high abundance of *Ap. caliginosa* in TURF sites indicates its high tolerance for a range of land covers and soil conditions (Lee, 1985). This endogeic species enters obligatory summer diapause (Lee, 1985) enabling its survival in adverse conditions. In Helsinki and Lahti, the presence of the epigeic *D. octaedra* in the woody REM and REF sites is associated with the tolerance of this species to low soil pH (Lee, 1985). By contrast, *L. terrestris* occurred in all soil habitats. While the general

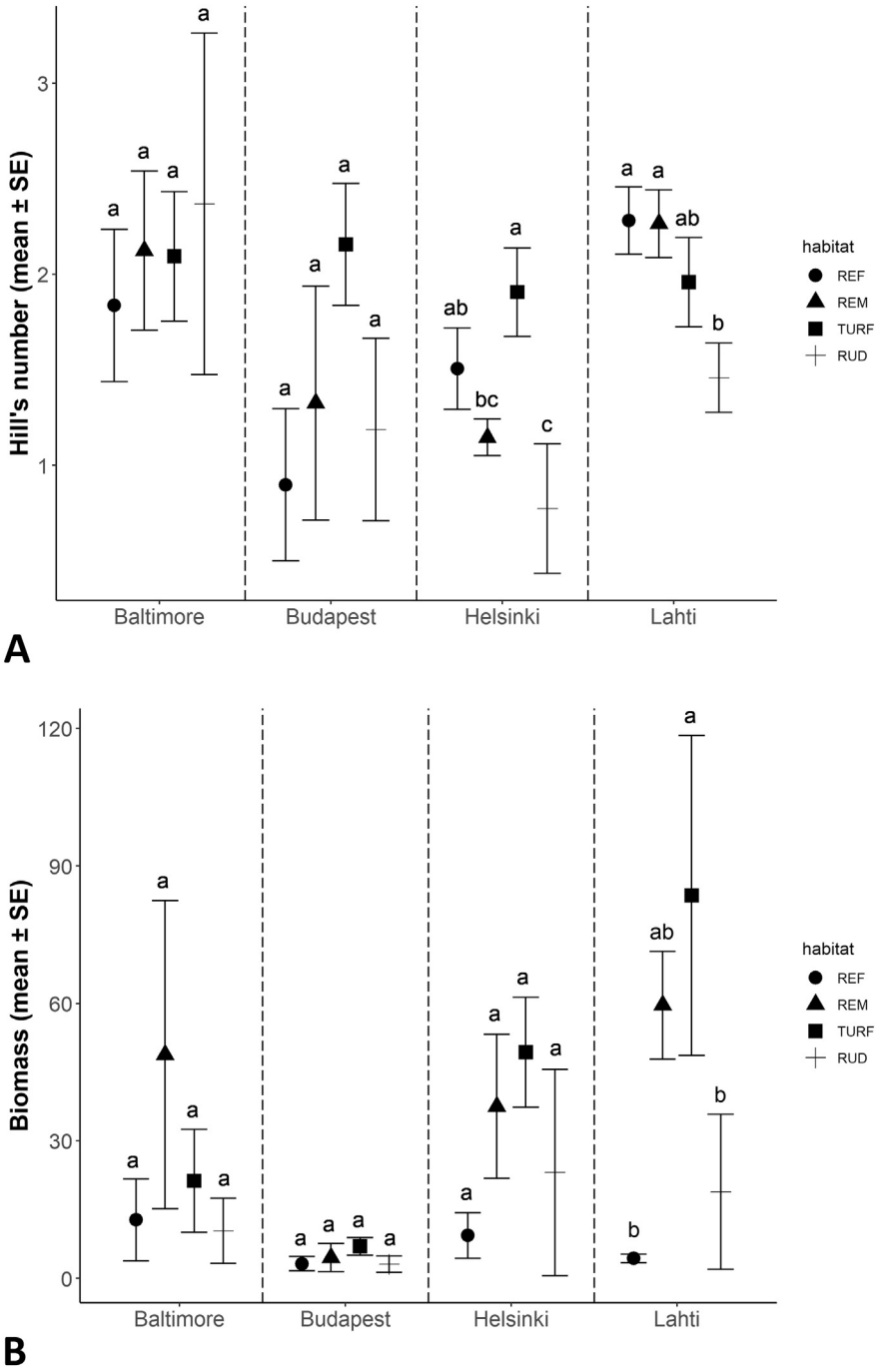

Fig. 1. Diversity (Hill's number, A) and biomass (fresh mass; g m^{-2}, B) of earthworm communities in four soil habitat types in four cities. Different letters indicate significant differences between habitat types, based on general linear models. Each city was analyzed separately. REF: reference; REM: remnant; TURF: turf/lawn; RUD: ruderal.

perception of this species is that of an anecic earthworm, which needs deep soil to build vertical burrows, and leaf litter as a food resource, *L. terrestris* has been shown to exhibit high plasticity both for food resources (Zicsi et al., 2011) and soil habitat type (Zeithaml et al., 2009), as well as behavioral plasticity, for instance in terms of cast deposition and depth of burrowing (Paul et al., 2012; Zicsi et al., 2011).

The well-documented alteration in urban soil properties appear to be less relevant to earthworm communities. Lower soil organic carbon was not a driver, partly because the SOC concentrations in our study sites (Pouyat et al., 2015) remained within the tolerance ranges of earthworms (Lee, 1985). As for soil pH, several previous studies have shown that urban soils typically have higher pH, which has been associated with materials used in urban infrastructure that are high in calcium, such as concrete (Pouyat et al., 2007; 2015). This factor might positively influence earthworms especially in regions with acidic native soils. Even more important in this case is the quality and quantity of food resources. Coniferous forests, often with a thick uppermost organic layer composed of recalcitrant plant material lacks earthworms or have low abundance of a few tolerant species (Addison, 2009). Remnant forest patches in boreal cities are often a mixture of conifers and broadleaved species; for instance, small-leaved linden (*Tilia cordata*) and Norway maple (*Acer platanoides*), providing high quality food for litter feeding species.

The high degree of similarity observed in the urban fauna indicates

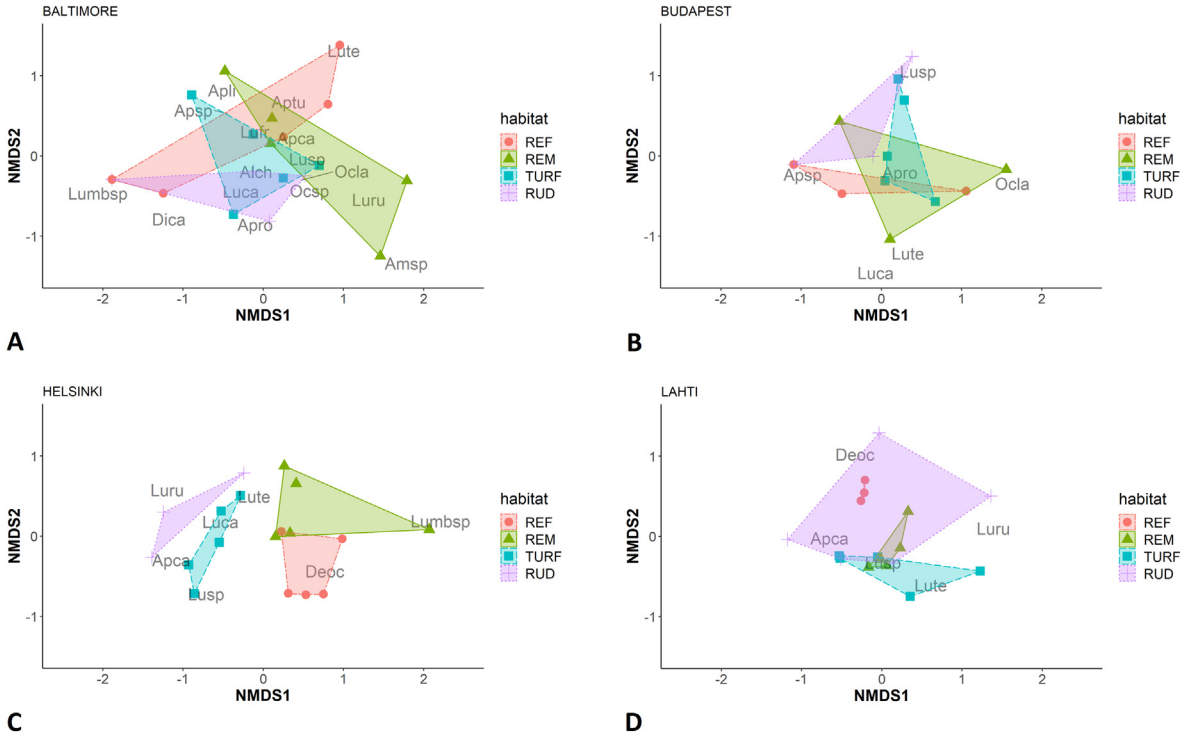

Fig. 2. Non-metric multidimensional scaling (NMDS) ordination plots based on Bray Curtis dissimilarities of earthworm communities by soil habitat types in four cities (A-D). REF: reference; REM: remnant; TURF: turf/lawn; RUD: ruderal. For full species names, see Table 2.

biotic homogenization. Biotic homogenization in general and especially in cities is associated with two processes: extinction of local species, and introduction of non-native species (McKinney, 2006; Olden, 2006). The underlying assumption is that a native species pool, determined by regional climate, geography and long-term history, exists surrounding the city. Aronson et al. (2016) added land use history as a major factor determining present day regional species pools. Consequently, urban flora and fauna are shaped through various physical, biological and socio-economical filters, as well as human facilitation (Aronson et al., 2016; Swan et al., 2011). Clearly, the relative importance of these drivers influencing earthworm assemblages at different locations varies. While peregrine species dominate urban earthworm communities, resulting in high similarity among cities, to better understand the mechanisms leading to this similarity, it is necessary to evaluate historical and biogeographical changes in each regional species pool.

As for many Northern regions in Europe and North America, Finland lacks endemic species due to Quaternary glaciations, thus there is no 'native' regional species pool. The present-day earthworm fauna is the result of human introductions since the early Holocene, rather than natural northward expansion after the last Ice Age (James, 1998). As a result, the entire fauna of Finland consists of 15 species (excluding greenhouse and domicole earthworms) (Blakemore, 2007; Terhivuo, 1988). Currently these peregrine species are restricted to human-modified habitats, because the natural vegetation of coniferous forests and associated soil properties, such as low pH, impedes the spread of these species. However, future changes in climatic conditions, as well as land use, may facilitate earthworm colonization (Cameron and Bayne, 2009; Moore et al., 2018) from densely populated areas to wildlands.

The potential regional species pool for Budapest is rich, with approximately half of the species being autochthonous, i.e. not introduced (Table S2). In the city, 16% of this pool was recorded, and the list substantially overlaps with the fauna of Finnish cities, which lacks a

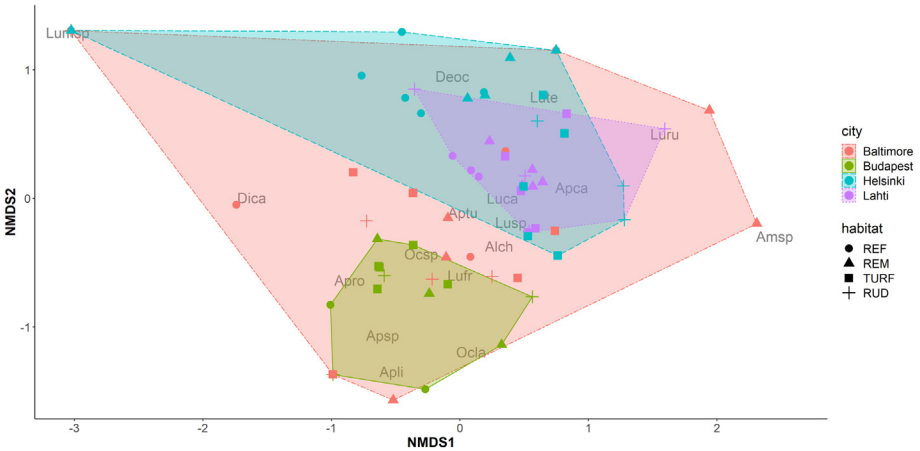

Fig. 3. Differences in earthworm community composition by soil habitat types and biogeographical regions (city). REF: reference; REM: remnant; TURF: turf/lawn; RUD: ruderal. For full species names, see Table 2.

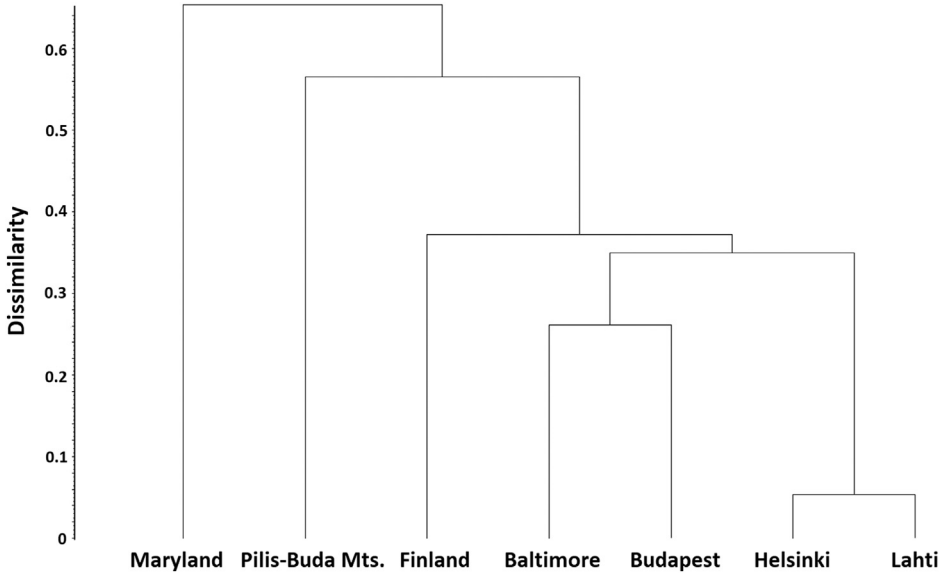

Fig. 4. Comparison of species composition at the city scale to the regional species pools using the Baroni-Urbani and Buser similarity index. Cities and their respective regional species pools are Baltimore/Maryland, Budapest/Pilis-Buda Mts., and Helsinki and Lahti/Finland. See Supplementary Table S2 for the list of species.

native species pool. The underlying reason for the unexpectedly low species richness and abundance in the Budapest REF forests is edaphic. While the high pH, SOM and Ca content are favorable for earthworms, the soil is extremely shallow. The depth to the parent material is 10–30 cm, consequently, soil moisture is low throughout the year. Additionally, some of the forest stands were dominated by sessile oak (*Quercus petraea*), which produces unpalatable litter for earthworms (Zicsi et al., 2011).

Due to its distinct biogeographical position, we expected the reference forests in Baltimore to significantly differ from the urban habitat types. There are two North American native lumbricid genera (*Eisenoides* Gates, 1969 and *Bimastos* Moore, 1893) as well as the genus *Diplocardia* Garman 1888 (Acanthodrilidae) in the regional species pool. Contrary to expectation, peregrine lumbricids dominated even the reference forests. Historical land use partly explains this pattern: almost all forests in the region are secondary forests, recovering from logging and agriculture (Brush, 1986; Chang et al., 2016; Cooper, 1995). This legacy of land use history is reflected in the current earthworm fauna even in 100+ year old secondary forests (Szlavecz et al., 2018a). Additionally, due to their behavior and microhabitat preferences, some native species are more difficult to catch using the standard quadrat method. For example, most *Bimastos* spp. are found under the bark of decaying logs or in wetlands (Csuzdi et al., 2017); *Eisenoides lonnbergi* is primarily a riparian and wetland species (McCay et al., 2017), and most *Diplocardia* spp. are endogeic oligohumic, and do not readily emerge with mustard extraction.

Another group of introduced species, the Asian pheretimoids, represent a second wave of earthworm invasion (Chang et al., 2018; Szlavecz et al., 2018a). In the present study, pheretimoids were detected only in Baltimore. Although juvenile *Amynthas* spp. were recorded only in the REM forests, at least three species in this group are known from various locations and habitat types within the geographic location (Chang et al., 2018). Being annual species, pheretimoids appear as small juveniles in spring, which is the best season for collecting lumbricids. In order to properly assess their presence in urban green spaces, late summer sampling needs to be added to the surveys. To date, pheretimoids in Hungary and Finland are only known from greenhouses (Csuzdi et al., 2008; Terhivuo and Valovirta, 1974). As pheretimoid invasion is currently ongoing in many regions (Chang et al., 2018), we expect global range expansion and spread of these earthworms even into undisturbed ecosystems (Brown et al., 2006).

5. Conclusions

Our results show that properties of urban soil habitat types affect earthworm communities, even though they were not sensitive to specific edaphic factors tested in this study. This indicates that other variables, for example soil moisture and the quality of food resources, might be more important in shaping communities. While we did not find a geographically uniform driver that best explains the most suitable habitat for earthworms, public green spaces such as turf/lawn and remnant forests seemed to be important for maintaining abundant urban earthworm communities.

Despite the clear differences in climate, soils and biogeography among the studied cities, the earthworm fauna showed remarkable similarity between cities, but this similarity is a result of the combination of different geographical and human history. Local extinction of native fauna, a component of biotic homogenization, has not happened in Finland because there was none. Introduction of non-natives to North America was an important step regionally, because it involved crossing a major geographical barrier. However, the introduction of non-native species to Baltimore is not an urban phenomenon, because the surrounding landscape is also dominated by peregrines. Despite all these differences, human facilitated dispersal both at regional and local scales, as well as site modification and alteration of microenvironmental conditions at the local scale, appear to be key in shaping urban earthworm communities.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Table 4
Peregrine earthworm species records in cities. × indicates presence. Only species overlapping with the present study are listed.

Species	Basel Switzerland	Bonn Germany	Brno Czech Republic	Brussels Belgium	Dorsten Germany	Greifswald Germany	London UK	Moscow, ID USA	Warsaw Poland	Zurich Switzerland
Allolobophora chlorotica	×	×	×	×	×	×	×		×	×
Aporrectodea caliginosa	×	×	×	×	×	×	×		×	×
Aporrectodea limicola		×		×					×	
Aporrectodea rosea	×	×	×	×		×				
Aporrectodea tuberculata										×
Dendrobaena octaedra		×	×	×	×	×				×
Lumbricus castaneus	×	×		×	×	×	×		×	×
Lumbricus friendi										
Lumbricus rubellus	×	×	×	×	×	×	×	×	×	×
Lumbricus terrestris	×	×	×	×	×	×	×	×	×	×
Octolasion lacteum	×	×	×	×		×	×		×	
Source	Glasstetter and Nagel, 2001	Fründ and Ruszkowski, 1989	Schlaghamerský and Pižl, 2009	Pižl and Josens, 1995	Keplin and Broll, 1997	Unger, 1999	Smith et al., 2006	Smetak et al., 2007	Pilipiuk, 1981	Tresch et al., 2019

earlier versions of the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2020.103530.

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